THE YOUNG ONES — SMALL TEMNOSPONDYLS FROM THE ARCADIA FORMATION

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An assemblage of small temnospondyl (Amphibia, Labyrinthodontia) skulls from the Arcadia Formation of Queensland is the only such collection from the Early Triassic. Using non-morphometric characters we have been able to identify, from among these specimens, juvenile capitosaurs and a rhytidosteid, whereas two skulls of similar size and superficially similar shape have been determined as mature dissorophoids. We caution against the use of skull proportions in labyrinthodont taxonomy and demonstrate that the trematosaurian group of labyrinthodonts can be considered to be neotenic in at least one character.

☐ *Amphibia, Labyrinthodontia, temnospondyls, Triassic, Arcadia Formation, capitosaurs, rhytidosteid, juveniles.*

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One problem common to palaeontological and neontological studies of the Class Amphibia s the difficulty of determining to which known adult species a juvenile might belong. Small labyrinthodont amphibians of the order Temnospondyli are commonly found at several localities in the Permo-Carboniferous of Europe and the middle Pennsylvanian of Illinois. Originally assigned to the labyrinthodont Order Phyllospondyli, or branchiosaurs, these were recognised by Romer (1939) as having the characteristics of small or larval temnospondyls. While some of these Palaeozoic forms may now be assigned to various genera within the Eryopoidea and Trimerorachoidea, most remain sheltered beneath the enlarged umbrella of the Dissorophoidea.

The Early Triassic Arcadia Formation of Queensland has yielded a series of labyrinthodont fossils belonging to various families of temnospondyls. Most common components of the labyrinthodont fauna are members of the families Capitosauridae (Warren 1980; Warren & Hutchinson, 1988), Rhytidosteidae (Howie, 1972a; Warren & Black, 1985; Warren & Hutchinson, 1987), Brachyopidae (Howie, 1972b; Warren & Hutchinson, 1983) and Chigutisauridae (Warren, 1981). Rare and fragmentary specimens of the Trematosauridae (Warren, 1985b) and Plagiosauridae (Warren, 1985a) have also been found. In addition, the material collected from the Arcadia Formation includes a number of small skulls of rather uniform size and shape which initially proved difficult to place in a known family. These presumed juveniles are the smallest (youngest?) individuals to be recorded from the Triassic. Much larger juveniles of near-adult proportions have been described in the Triassic species *Benthosuchus sushkini* (Bystrow & Efremov, 1940) and *Parotosuchus peabodyi* (Welles & Cosgriff, 1965).

When considering the relationships of the Queensland juveniles we need to look at the families of Triassic temnospondyls known from Australia and must also consider the possibility that, as in the Palaeozoic, some specimens may be adults of small temnospondyl species such as those found within the Dissorophoidea.

CAPITOSAURIDAE

The first enlightenment came in 1984 when we discovered at the Duckworth Creek locality some one centimetre long skulls (QMF 12290, QMF 12291) in close proximity to remains of moderately-sized temnospondyls (QMF 12281, QMF 12282). Although the characteristic capitosaurid skull shape was not evident, so that the larger skull showed the proportions of a lydekkerinid while the smaller resembled a branchiosaur (Fig. 1), we soon realised that skulls of both sizes shared several characters of the Family Capitosauridae. In both we were able to recognise capitosaurid features such as the hamate process of the lower jaw, transverse ridges on the parasphenoid, inclusion of frontal bones in the

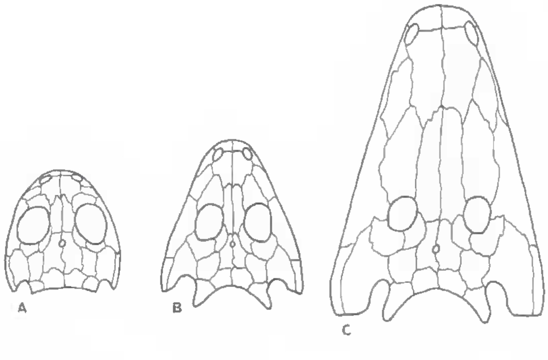

FIG. 1. Differences in proportions between the dorsal skull roofs of: A. *Parotosuchus aliciae* (QMF 12291), B. *Parotosuchus aliciae* (QMF 12281), C. *Parotosuchus gunganj*. All three specimens drawn to the same orbital length; scale bar = 1 cm.

orbits, well-developed falciform crest of the squamosal, and an oblique ridge on the pterygoid. Within the Capitosauridae the specimens could only belong to the genus *Parotosuchus,* with otic notches widely open posteriorly. It is also apparent that the two are conspecific, sharing an extremely hypertrophied oblique ridge on the pterygoid, the absence of a crista tabularis externa beneath the tabular horn, and the presence of ectopterygoid tusks. We have described them as *P. aliciae* (Warren & Hutchinson, 1988).

On criteria used by Boy (1974), the smallest *P. aliciae* skulls may be determined as immediately post-metamorphic individuals, since there is no trace of a branchial skeleton, whereas the larger are young adults. The apomorphies of *P. aliciae* are not found in either of the other species of *Parotosuchus* from the Arcadia Formation, *P. gunganj* and *P. rewanensis* (Warren, 1980). It appears that a mature adult of *P. aliciae* has not yet been found.

Enormous allometric changes accompany the growth of *P. aliciae* from the smallest individual to a mature capitosaur. Therefore, unless it can be demonstrated that a specimen is adult, morphometric features such as skull proportions, position and shape of orbits, length or width of individual skull bones, size of otic notch, depth of skull, and so on, should not be used to determine species, genera, or even families. For instance, if overall proportions were accepted as a valid criterion, the youngest *P. aliciae* skull could, be placed in the Dissorophoidea, the Chigutisauridae or the Rhytidosteidae, but certainly not in the Capitosauridae.

We have identified several other partial skulls as being juvenile capitosaurs, belonging to the genus *Parotosuchus* but not to *P. aliciae*. All are of juvenile size and shape, with large orbits, and all have one or more of the capitosaurian features mentioned above. Of these the most easily observed are the falciform crest of the squamosal and the inclusion of the frontal in the orbital margin. That this frontal inclusion is not itself a juvenile feature of temnospondyls, as might be inferred from Watson's implied growth series of *Onchiodon* (1963, fig. 1), is shown by some later studies of Palaeozoic dissorophoids and eryopoids; examples include *Amphibamus grandiceps*, a primitive larval dissorophid from Mazon Creek, Illinois (Milner, 1982), and *Sclerocephalus* sp. (Boy, 1974), an eryopoid, both of which have the frontals excluded from their orbits.

One unexpected feature of all the *P. aliciae* skulls is the presence on the occipital surface of a palatoquadrate fissure between the ascending ramus of the pterygoid and the squamosal. This was one character used by Warren and Black (1985) to divide most of the Triassic temnospondyls into two groups — a trematosaurian group (Trematosauridae, Rhytidosteidae, Brachyopidae, Chigutisauridae, Lydekkerinidae), in which the fissure is present, and a capitosaurian group (Rhinesuchidae, Uranocentrodontidae, Benthosuchidae, Capitosauridae, Mastodonsauridae, Almasauridae, Metoposauridae), in which it is absent. The presence of the palatoquadrate fissure in immature capitosaurids indicates that it may now be regarded as a juvenile character whose retention in the adult (or in larger specimens) is apomorphic for the trematosaurian group. Trematosaurians may thus be considered paedomorphic, and probably neotenic (*sensu* McNamara, 1986), in their expression of the palatoquadrate fissure. The fissure is apparently absent from Permian outgroups (Eryopoidea, Trimerorachoidea), although it does appear in the neotenic *Dvinosaurus* (Bystrow, 1938). By analogy with juvenile capitosaurs, trematosaurians are also neotenic in the absence, or weak development, of the tabular horns, and in some families, in the parabolic skull shape and large orbits.

RHYTIDOSTEIDAE

Another of the tiny skulls from Duckworth Creek, QMF 12293 (Fig. 2), appears not to have

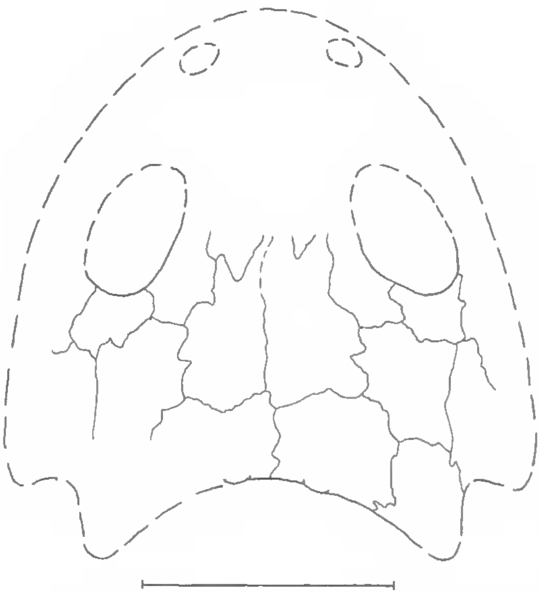

FIG. 2. Juvenile rhytidosteid skull (QMF 12293) in dorsal view. Provisionally referred to *Arcadia myriadens*. Scale bar = 1 cm.

had the frontal included in the orbital margin. It has pointed, widely-spaced tabular horns, a broad palate without the transverse ridges characteristic of capitosaurids, and its pterygoid and parasphenoid are highly denticulate. These are all characteristic features of the Family Rhytidosteidae. In addition, its ornament is finely textured, with many foramina entering the valleys between the ornament ridges. Similar foramina were noted by Cosgriff and Zawiskie (1979) as characteristic of some rhytidosteids, and were present also in *Arcadia myriadens* (Warren & Black, 1985). QMF 12293 is from the same locality as *A. myriadens*, and, although their ornament is differently textured, it is possible that this difference is ontogenetic. The skulls share two raised areas of ornament on the posterior skull margin, a feature not found elsewhere among rhytidosteids, and both apparently lack a parietal foramen. We refer QMF 12293 provisionally to *Arcadia myriadens* within the family Rhytidosteidae.

DISSOROPHOIDEA

Finally, two skulls (QMF 12284, 12285) with associated postcranial material from the Crater (field locality L78) have been identified as members of the superfamily Dissorophoidea (Warren & Hutchinson, in prep.; Fig. 3). This assignment is not without reservation as the skulls have features seen in no known dissorophoid and lack some which are characteristic for most members of the superfamily. Cranial characters which define dissorophoids, or have developed within the superfamily, and are present in QMF 12284 and QMF 12285 are: absence of lateral lines, large orbits and interpterygoid vacuities, basipterygoid joint fused but very narrow, parasphenoid plate without muscle crests or 'pockets', very large otic notch extending from tabular to quadrate, inclusion of frontals in the orbital margin, and an intervomerine depression. As well, various features of their postcranial skeleton, such as the reduced clavicle and gracile femur, indicate terrestriality, a way of life found in many dissorophoids. Of these various characters only the large interpterygoid vacuities and orbits have been identified as possible juvenile features (Boy, 1972). The two characters of our specimen which are particularly undissorophoid-like are the absence of a lachrymal and the (perhaps associated) lack of a lateral exposure of the palatine (LEP, Bolt, 1974). This lateral exposure was not universally present in dissorophoids but the absence of a lachrymal appears to be unique.

Within the Dissorophoidea our form is closest to *Micropholis stowi* (Boy, 1985), with which it shares an Early Triassic time-slot and Gondwanan distribution. In forthcoming work we propose to treat QMF 12284 and QMF 12285 as members of a new genus and species within the family Micropholidae (Warren and Hutchinson, in prep.).

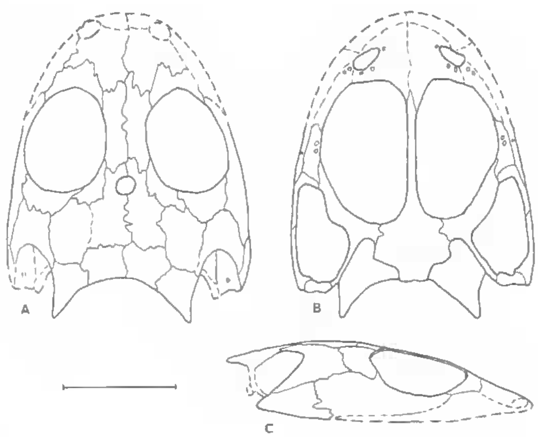

FIG. 3. Dissorophoid (QMF 12284) in A. dorsal, B. ventral, C. lateral views. Scale bar = 5 mm

CONCLUSIONS

Three results of this study are especially significant. First, it is often possible using apomorphic characters to identify, at least to family level, young juveniles of Triassic labyrinthodonts. Second, unless it can be determined that a specimen is adult, morphometric features such as skull proportions, position and shape of orbits, length or width of individual skull bones, size of otic notch, depth of skull etc., should not be used to determine species, genera, or even families. Third, the trematosaurian group of Triassic temnospondyls may be considered neotenic in the retention of a palatoquadrate fissure in the adult.

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